Comparative Morphology of the Eyes of Postlarval Bresiliid Shrimps From the Region of Hydrothermal Vents

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Abstract. The structure and ultrastructure of the eyes of postlarval vent shrimps provisionally designated '*Alvinocaris*' and '*Chorocaris*' are described. The eyes of the postlarval '*Alvinocaris*' are cylindrical, borne on short stalks, and contain closely packed rhabdoms. The ommatidia lack dioptric apparatus and have rhabdoms extending almost to the cornea. The rhabdoms consist of orthogonal layers of microvilli typical of crustacean rhabdoms. The eyes of the '*Chorocaris*' are similar, but the rhabdom layer extends back through the reduced eyestalks and covers some of the dorsal surface of the cephalothorax. The rhabdoms from both the anterior and the thoracic regions consist of layered microvilli. The eyes of a slightly smaller postlarval vent shrimp, termed 'Type A', differ. Although clearly related to the other vent shrimps, Type A has stalked eyes held at an angle to the head. The eye displays a gradient of ommatidial development, with the older ommatidia closely resembling those seen in the other postlarval types. Between the cornea and the rhabdom layer, the youngest ommatidia possess quadripartite crystalline cones similar to those seen in related families of caridean shrimps; these are absent in the more mature ommatidia. The external structure of the anterior and thoracic eyes of juvenile *Rimicaris exoculata* (after settlement at the vent site) is also described. Juveniles up to 9 mm in carapace length have anterior corneas similar to those seen in postlarvae, whereas in larger specimens the corneas are progressively replaced by an ocular plate.

Introduction

Hydrothermal vents are generally found in the region of tectonic plate boundaries such as the mid-Atlantic ridge and the Galapagos rift. The emission of super-heated water (350°C) rich in minerals has led to the establishment of communities of animals that live around these vents and feed primarily on chemoautotrophic bacteria (Segonzac *et al.*, 1994). Such communities are dominated on the mid-Atlantic ridge by caridean shrimps of the family Bresiliidae (Williams and Rona, 1986). In the present study, the structure and ultrastructure of the eyes of postlarval shrimps obtained in the dark by trawling above a vent field in the mid-Atlantic ridge are described. In addition, the progressive reduction in size and disappearance of the anterior eyes during development is described in juvenile specimens of *Rimicaris exoculata* obtained from two vent sites sampled using a submersible vehicle.

The commonest vent shrimps recorded from the mid-Atlantic ridge are *Rimicaris exoculata, Chorocaris chacei,* and *Alvinocaris markensis* (Segonzac *et al.*, 1994), although there may be other species present. Although lacking conventional compound eyes, adult specimens of *R. exoculata* possess a large white photosensitive organ (thoracic eye) beneath the dorsal surface of the carapace (Van Dover *et al.*, 1989). It has been suggested that this thoracic eye is used for detecting light emitted from the vents (Pelli and Chamberlain, 1989; Van Dover *et al.*, 1994). In the present study we found that, in their early stages, postlarval *R. exoculata* possess eyes of a conventional appearance, but that these gradually disappear during development. Because the eyes do not contain any dioptric apparatus during the later stages of development,

they are referred to below as anterior eyes (if located in the position normally occupied by the eyestalks) and dorsal or thoracic eyes (if located on the dorsal surface of the cephalothorax). The structure of the thoracic eye has been described for *R. exoculata* (O'Neill *et al.*, 1995) and for a new unidentified species of *Rimicaris* (Nuckley *et al.*, 1996). The evolutionary origins of the thoracic eye are not immediately obvious, although possible clues to its provenance may come from studies of vent shrimps possessing eyes of a more conventional appearance. *Alvinocaris markensis* has no thoracic eye but does possess small anterior eyes, although it has been reported that the latter contain no photoreceptors (Wharton *et al.*, 1997). *Chorocaris chacei* and *Chorocaris fortunata* not only have reduced anterior eyes but also have thoracic eyes that may be contiguous with them (Lakin *et al.*, 1997; Kuenzler *et al.*, 1997). Hypotheses about the relationship of the thoracic organ to the usual decapod compound eye have been put forward (O'Neill *et al.*, 1995; Nuckley *et al.*, 1996; Lakin *et al.*, 1997; Kuenzler *et al.*, 1997), but the development of vent shrimp eyes has not been investigated. In the current study, the structure of both anterior and thoracic eyes is described in various postlarval and juvenile stages of vent shrimps. The term *postlarvae* is used here to designate post-zoeal stages bearing the full complement of abdominal appendages (Herring and Dixon, 1998).

Because the eyes of deep-sea decapod crustaceans are adapted to maximize sensitivity, they are susceptible to light-induced damage when they are exposed to light levels significantly higher than ambient (Loew, 1976; Shelton *et al.*, 1985). The damage manifests itself as irreversible rhabdom breakdown and changes to other structures in the eye (Gaten *et al.*, 1990). The thoracic eyes of adult vent shrimps described at the ultrastructural level in previous studies were obtained from animals that had been illuminated by the floodlights of a submersible vehicle during capture and sometimes by other light sources afterwards (O'Neill *et al.*, 1995; Nuckley *et al.*, 1996; Lakin *et al.*, 1997; Kuenzler *et al.*, 1997). This is likely to lead to light-induced structural damage, making it difficult to be certain that the appearance of the rhabdoms in such material is normal. Thoracic eye rhabdoms are described as lacking the orthogonally orientated layers of microvilli typical of rhabdoms in other Crustacea, and they often contain irregular arrays of microvilli—some of which may be expanded to form vesicles within the rhabdom (Van Dover *et al.*, 1989; O'Neill *et al.*, 1995; Nuckley *et al.*, 1996; Kuenzler *et al.*, 1997). To confirm that this appearance is not artifactual, it is necessary to examine material that has not been exposed to visible light. The postlarval shrimps used for ultrastructural analysis in the present study were obtained by trawling. Consequently

they had not encountered lights from a submersible vehicle, and they were not exposed to white light at any stage during capture. This has enabled us to investigate rhabdom structure in specimens that have definitely not been damaged by light. The results show that in the postlarval stages at least, the rhabdom structures in both anterior and thoracic eyes have the banded appearance typical of other crustaceans.

The shrimps we examined were taken from a collection made during a mid-Atlantic survey carried out during Charles Darwin cruise 95 (Herring, 1996). Although no classification of postlarval bresiliid shrimps is currently available, the collection was found to contain three morphologically distinct types: postlarvae of the genus *Alvinocaris*, a group classified as 'Chorocaris' type, and a group of morphologically indistinguishable younger postlarvae that were arbitrarily designated 'Type A' (Herring, 1996). A DNA analysis of selected specimens from the collection concluded that the *Alvinocaris* postlarvae were probably *A. markensis*, while those identified as 'Chorocaris' type postlarvae were indeed mainly *Chorocaris* sp. but included occasional specimens of *Rimicaris* (Dixon and Dixon, 1996). The same study found that the Type A specimens included individuals from three genera: *Alvinocaris*, *Chorocaris*, and *Rimicaris*. Whatever the final assignation of the specimens, the present paper represents the first description of developing stages of anterior and thoracic eyes in vent shrimps. It also shows that the thoracic eyes are anatomically continuous with the anterior eyes in postlarval stages and are almost certainly derived from them.

Materials and Methods

Most of the postlarval shrimps described were obtained by trawling above a known hydrothermal vent site (Broken Spur—29°10'N) in the mid-Atlantic ridge (segment 17) during cruise 95 of the RRS *Charles Darwin*. The maximum depth in the region of the vent field is 3200 m. A multiple rectangular midwater trawl (Roe and Shale, 1979) was used to fish the nets above the vent region at depths ranging from 2000 to 3050 m. A total of 232 postlarval vent shrimps, all between 13 mm and 23 mm total length, were taken, mostly within 1000 m of the vent. Although abundances decreased both vertically and horizontally away from the vents, some shrimps were taken at more than 100 km from known vents (Herring, 1996). The nets were hauled after dark, the opaque codends were protected from light, and the shrimps were sorted under dim red light to avoid light-induced damage.

Whole shrimps, heads, or eyes were fixed in the dark in 3% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2. Some specimens were embedded on board ship (through

a graded ethanol series and into Taab E-Mix resin *via* propylene oxide), whilst others were stored in fixative and embedded ashore up to 3 months later (dehydrated in acetone and embedded in Spurr's resin). Semithin (1 μm) sections were taken for light microscopy and pale gold sections for electron microscopy. Semithin sections were stained in 1% toluidine blue in 4% borax and mounted in resin under a thin coverslip. Ultrathin sections were mounted on grids, stained by standard techniques in uranyl acetate and lead citrate, and observed on a JEOL CX100 transmission electron microscope. Other specimens were dehydrated, critical point dried in carbon dioxide, and coated with gold/palladium for observation using a Cambridge S100 scanning electron microscope.

Quantitative measurements were made from both electron micrographs (diameters of microvilli) and light micrographs (rhabdom volume density and microvillar surface area). To determine the rhabdom volume density, rhabdom areas were measured on micrographs of transverse and longitudinal sections of the retinular cell layer and recorded as a proportion of the total area. The surface area of microvillar membrane was calculated assuming that the microvilli are cylindrical and hexagonally packed; the values are recorded as square micrometers of membrane per cubic micrometer of rhabdom.

A limited number of large juvenile shrimps were obtained by net from a submersible at the Broken Spur (29°10'N) and TAG (26°8.25'N) sites during the Russian/British BRAVEX/94 program. They were fixed in buffered formalin solution, without having been protected from light during capture.

Results

External appearance

The 'Chorocaris' type postlarvae (Fig. 1A) and the *Alvinocaris markensis* postlarvae (Fig. 1C) are similar in general appearance, differing primarily in the lengths of the rostra and in the presence of a thoracic eye in the former. 'Chorocaris' has anterior eyes that are almost cuboid, largely because the anterior medial surfaces of the two eyes are flattened where they abut each other and the ventral surfaces of the eyes are flattened where they abut the underlying carapace. The lateral and anterior surfaces of the eye are also relatively flat. Both anterior eyes are almost hidden beneath the short, blunt rostrum; they are sessile and, although separate at anterior levels, they are fused in the midline more posteriorly. A small papilla is present on the medio-dorsal region of the cornea. The anterior eyes do not show regular external facetting, but roughly square arrays of ommatidial units are visible in fresh specimens. This pattern extends seamlessly behind the eye and into the thorax, where the retina extends to form thoracic eye lobes on either side of the midline beneath the dorsal carapace. The thoracic eyes are white in freshly caught animals, but turn dark following extended fixation. The *Alvinocaris markensis* postlarvae have a long, pointed rostrum with anterior eyes that are rounded and sessile. They also possess a corneal papilla. There is no sign of any external facetting on the cornea (Fig. 1B) and no extension of the retina into the thoracic region to form thoracic eyes.

Type A postlarvae differ from the preceding types principally in the structure of the eyes. These are borne on eyestalks projecting forward at an angle of about 45° to the antero-posterior axis and are located on either side of the long, pointed rostrum (Fig. 1D). In this orientation the functional parts of the eye face laterally and anteriorly. The carapace covers most of the medial face of the eyestalk. As in the other two taxa, a papilla is present on each eyestalk. Scanning electron micrographs revealed traces of external facetting on the cornea even though the soft cornea in most of the specimens had been damaged during capture or subsequent processing. The facets are hexagonal over most of the eye (Fig. 1E), although some postero-ventral facets are square (Fig. 1F). There is no sign of a thoracic eye. The anterior eyes of the juvenile shrimps obtained from Broken Spur and TAG varied in the extent to which they were developed, with the smaller individuals possessing the most pronounced anterior eyes. In the largest specimens, anterior eyes were replaced by a fused ocular plate as in adult *R. exoculata* (Segonzac *et al.,* 1994). In addition to the variability in eye appearance, these specimens revealed differences in the degree of reduction of the rostra and the inflation and forward expansion at the rounded anterolateral margins of the carapace. They all possessed a thoracic eye, and the first cheliped had the slender shape and chela structure typical of *R. exoculata* (Williams and Rona, 1986). Although in certain respects they resembled juvenile *Chorocaris chacei,* the antennal scale completely lacked the external tooth characteristic of that species. In addition, they possessed rounded eyes rather than the cuboidal ones seen in juvenile *Chorocaris.* On the basis of the antennal scale characteristics and the structure of the first cheliped, we are confident that these juvenile vent shrimps obtained from the Broken Spur and TAG sites are *R. exoculata.* Because of their variable appearance, the anterior eye, carapace, and rostrum are not reliable characteristics for the separation of juvenile *Rimicaris* and *Chorocaris.* At the earlier postlarval stage, *R. exoculata* and *C. chacei* are morphologically inseparable but genetically distinct (Dixon and Dixon, 1996). As they mature, juveniles of *R. exoculata* apparently undergo a progressive reduction in the anterior eyes and rostra.
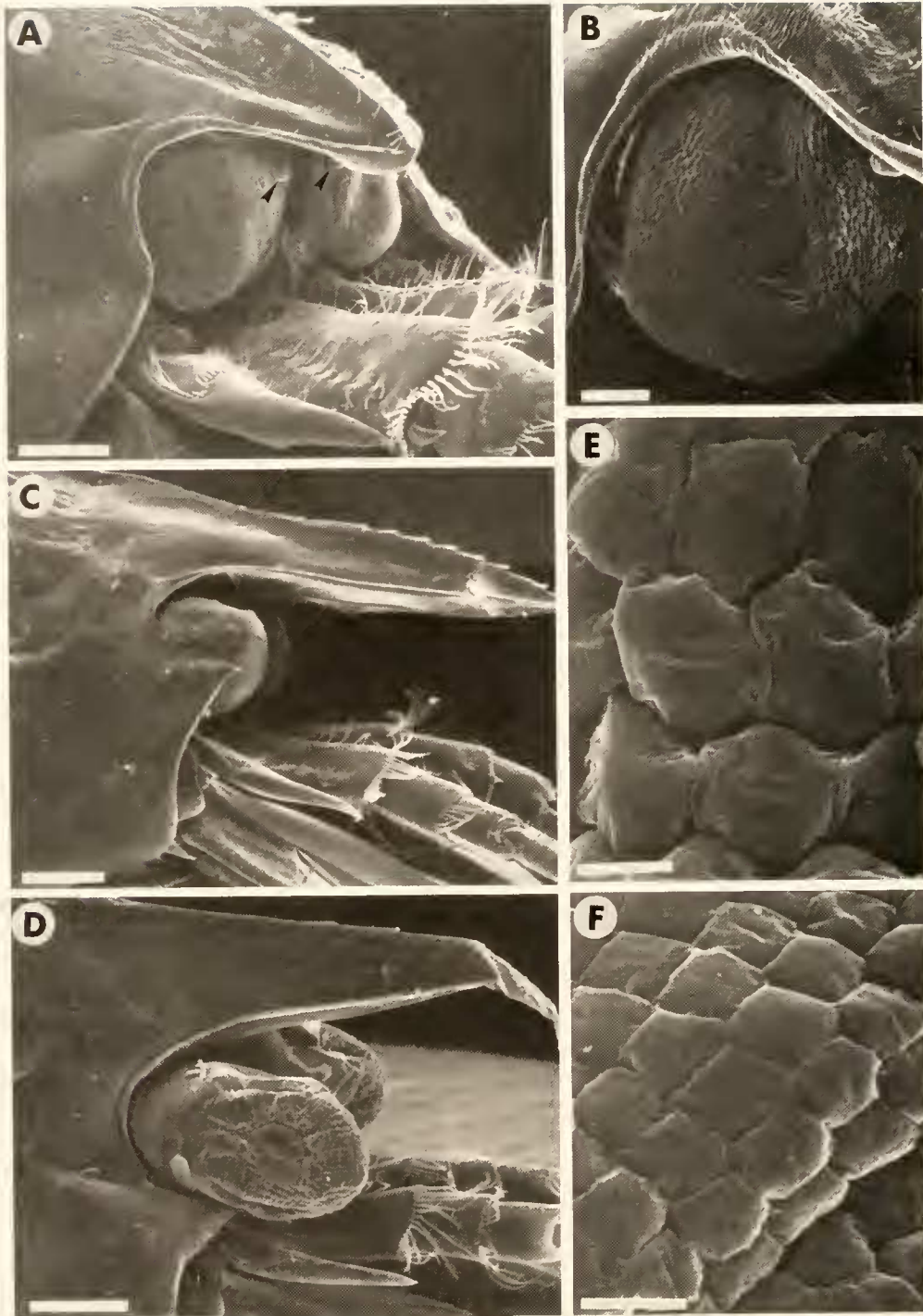
Figure 1.   Scanning electron micrographs of postlarval vent shrimps. (A) Antero-lateral view of '*Choro-caris*' showing the eyes almost hidden beneath the short blunt rostrum. Papillae (arrowed) are present on each eyestalk. (B) Anterior view of the right eye of the same species. Although the surface of the cornea is sculptured, there is no visible facetting. (C) Lateral view of *Alvinocaris* showing the much longer rostrum. (D) In this lateral view of Type A it can be seen that the eyestalks protrude either side of the long rostrum. External facetting is seen in this species, usually arranged hexagonally (E) but including areas of square facets ventrally (F). Scale bars: A = 250 μm, B = 100 μm, C = 500 μm, D = 500 μm, E = 25 μm, F = 50 μm.

Specimens up to 9 mm in carapace length retain distinct anterior corneas with the rostrum extending forward to their anterior limit (Fig. 2A). In larger specimens (carapace length 9.5 mm and above) the corneas are replaced by an ocular plate, and the rostrum is reduced and rounded (Fig. 2B). This reduction continues as the animals mature (Fig. 2C; carapace length 18 mm). Although adults of this species lack the cylindrical eyestalk seen in most caridean shrimp, it has been suggested that the ocular plate (Fig. 2C) is a reduced, flattened modification of the fused eyestalks of related vent shrimps (Martin and Hessler, 1990).

Internal structure

'Chorocaris' *type.* In sagittal sections, the anterior rostrum can be seen to extend forward over the anterior eye (Fig. 3A). The latter is bounded externally by a thin, unfacetted cornea anteriorly and laterally. However, where the cornea is opposed by carapace it is covered by extensive plumose cuticular protrusions. A thin layer of cells (presumed to be corneagenous cells) is present below the cornea (Fig. 3C). There are no crystalline cones. The rest of the eye is dominated by hypertrophied rhabdoms that fill most of the space between the cornea and the basement membrane (Fig. 3A, C). The rhabdom layer extends backward beneath the dorsal carapace of the cephalothorax without interruption to form the thoracic eye (Fig. 3A). The rhabdoms in all parts of the system are lobed, usually x-shaped in cross-section, and not arranged consistently in either a square or hexagonal array (Fig. 3B). Many of the rhabdoms within the anterior eye point in an anterior direction, with the result that vertical sections show rhabdoms with the same shape in cross-section (Fig. 3B). The rhabdoms in the thoracic eye are more variable in their arrangement but are usually at right angles to the carapace (Fig. 3C). Within the photoreceptor layer, the rhabdoms occupy about 75% of the available volume. The rhabdoms consist of microvilli that have a mean diameter of 0.079 μm (SD = 0.006; n = 20) and are arranged in alternating layers, both in the anterior eye (Fig. 3D) and in the thoracic eye (Fig. 3E). The microvilli are generally at right angles to the rhabdom surface, so each layer is not necessarily arranged orthogonal to the adjacent layer, especially in the dorsal eye. The average density of microvillar membrane was 50.8 μm^2/μm^3 of rhabdom.

A tapetum formed of reflecting pigment cells (creamy white in life) lies beneath the rhabdom layer, and the tapetal cells surround the bases of the rhabdoms (Fig. 4A, B). The retinular cells contain shielding pigment granules. Although a few of these granules may be found in the retinular cell cytoplasm adjacent to the rhabdoms, most of them are proximal to the photoreceptor nucleus and the tapetum (Fig. 4A). Lipid droplets are also abundant in the cells in this region. All of these cellular inclusions are found in both the anterior and thoracic parts of the visual system.
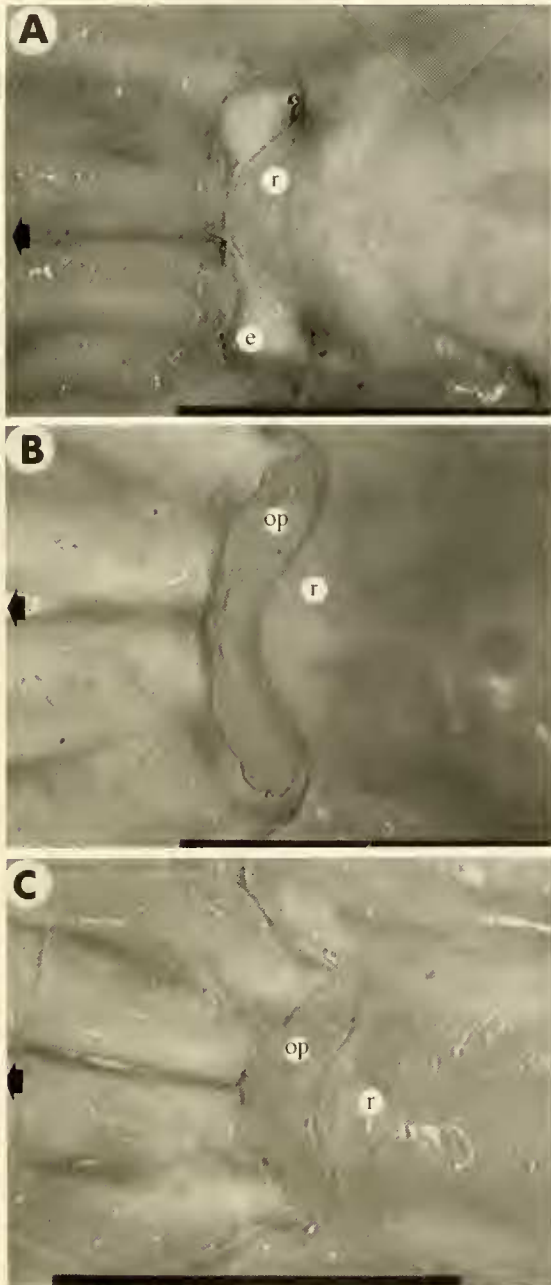

Figure 2. Light micrographs showing the dorsal view of the cephalothorax of *Rimicaris* sp. at various stages of development (arrow points to anterior). (A) Juvenile (9-mm carapace length) with separate eyes (e) and protruding rostrum (r). (B) Juvenile (9.5-mm c.l.) with fused ocular plate (op) and a reduced rostrum. (C) The reduction of the ocular plate and rostrum continues in the adult (18-mm c.l.). Scale bar: A = 2 mm, B = 2 mm, C = 5 mm.
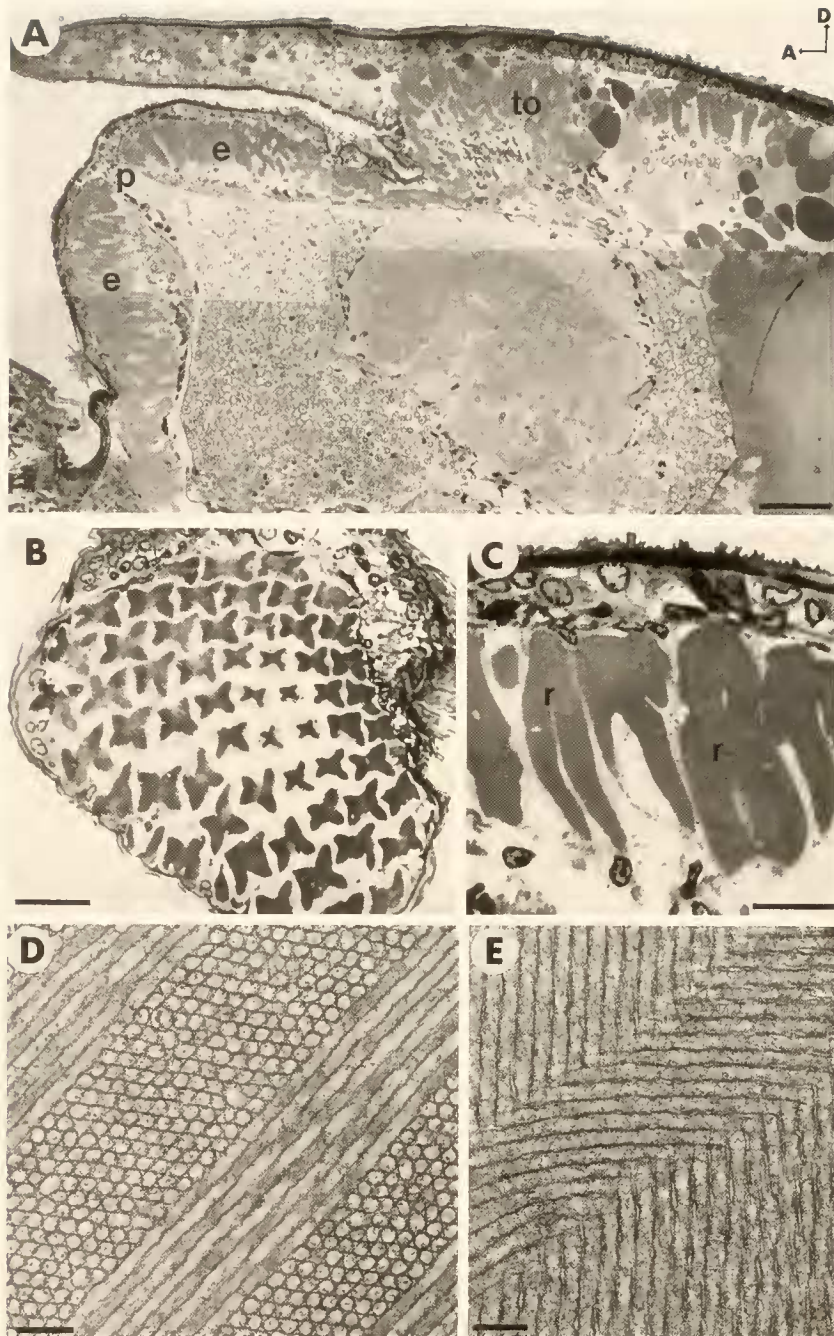
Figure 3. '*Chorocaris*' postlarvae (arrows point to Dorsal and Anterior). (A) Sagittal section showing rhabdoms extending in an almost uninterrupted row around the eye (e) and posteriorly beneath the dorsal carapace to form the thoracic organ (to). The only area in which rhabdoms are missing is where the connection from the sensory papilla (p) to the brain passes through the rhabdom layer. (B) Vertical section through the anterior region of an eye showing the x-shaped cross-sections of anteriorly directed rhabdoms. (C) Rhabdoms (r) in the thoracic organ (seen in longitudinal section) are irregular in shape and extend almost to the cornea. Electron micrographs of rhabdoms show the typical decapod layered arrangement of microvilli, both in the anterior eye (D) and in the thoracic organ (E). Scale bars: A = 100 μm, B = 100 μm, C = 25 μm, D = 0.2 μm, E = 0.2 μm.
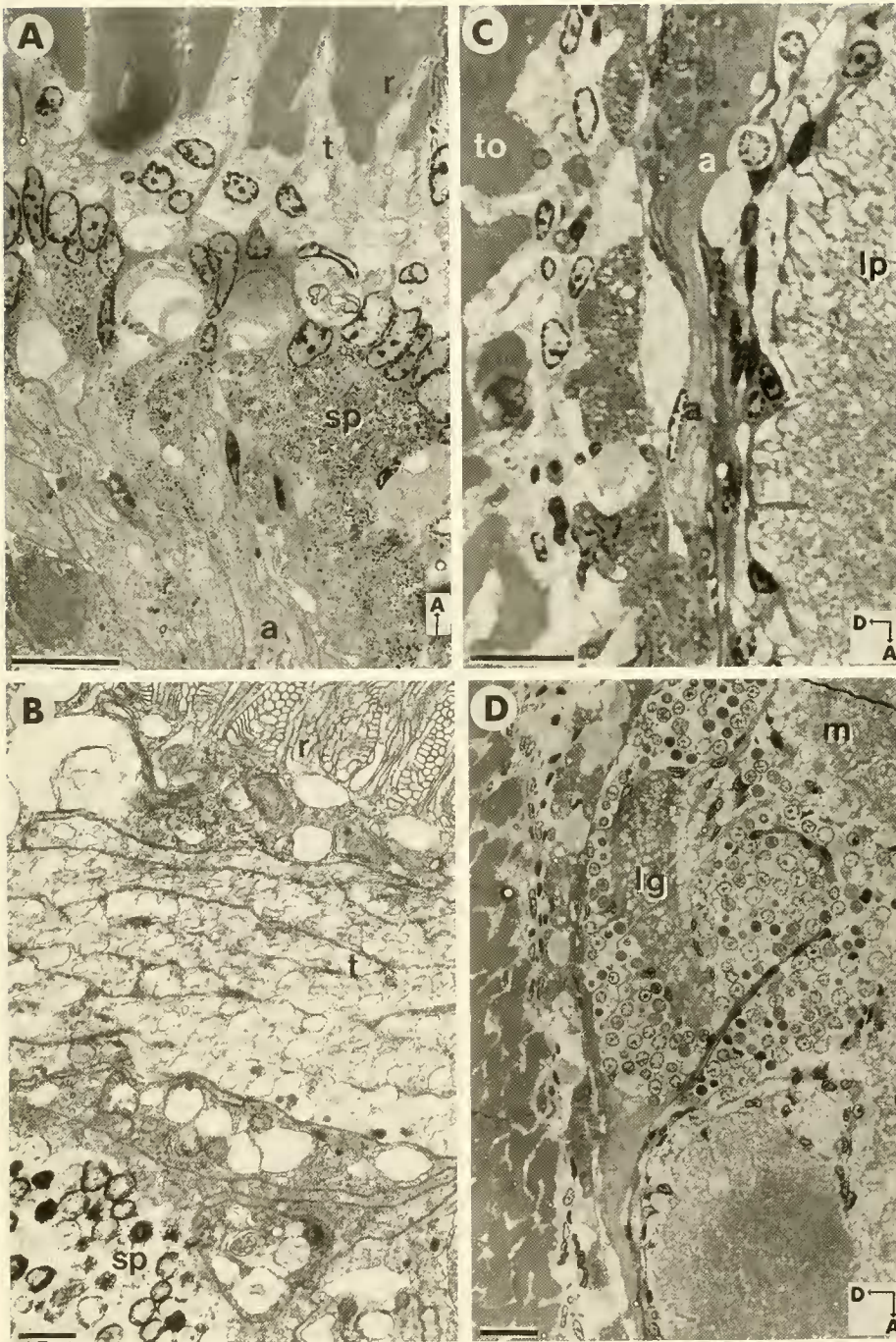
Figure 4. `Chorocaris` postlarvae (arrows point to Dorsal and Anterior). (A) Light micrograph showing the proximal rhabdom region (r), tapetum (t), proximal shielding pigment (sp), and the retinular cell axons (a). (B) Electron micrograph of a rhabdom (r), tapetal cell (t) and proximal shielding pigment (sp). (C) Posterior to the anterior eye, retinular cell axons (a) pass between the thoracic organ (to) and the lateral protocerebrum (lp). (D) The retinular axons eventually project onto the lamina ganglion (lg) and the medulla externa (m). Scale bars: A = 25 μm, B = 0.5 μm, C = 25 μm, D = 25 μm.

The retinular cell projection is modified in 'Choro-caris' by its distinctive brain morphology. In most decapods with stalked eyes, the optic neuropiles are located within the eyestalks in optic lobes that form the most anterior parts of the brain. They form outgrowths of the protocerebrum and lie immediately behind the eye, where they are innervated by retinular cell axons that pass directly through the basement membrane to project to the underlying lamina ganglion. In 'Chorocaris' postlarvae the eyestalks are greatly reduced and the optic neuropiles are within the main body of the protocerebrum. In addition, the optic lobes do not form the most anterior structure but are displaced posteriorly by the hypertrophied lateral protocerebral neuropile region with its associated cell bodies. It is this protocerebral region that lies immediately behind the basement membrane of the eyes. Because the optic neuropiles are displaced, the retinular cell axons have to travel a considerable distance posteriorly before reaching the lamina ganglion. Together the axons form a distinct optic nerve surrounded by neurilemma that is intimately associated with the basement membrane (Fig. 4C). On entering the protocerebrum, the optic nerve terminates in the lamina ganglion (Fig. 4D).

'Alvinocaris' *type.* The anterior eye is similar in general organization to that of 'Chorocaris'; the rhabdoms occupy much of the eye, and the crystalline cones are absent. However, in *A. markensis* the rhabdom layer does not extend into the cephalothorax to form a thoracic eye. The rhabdoms are more regular in outline than in 'Chorocaris' and are often square in cross-section (Fig. 5A). The rhabdoms occupy about 62% of the volume of the retinula cell layer. They point anteriorly over much of the eye with an interommatidial angle of around 3° (Fig. 5B) and taper posteriorly, where they are surrounded by seven retinular cells (Fig. 5C). The rhabdoms show the alternating, orthogonally orientated rows of microvilli characteristic of decapod crustacean eyes (Fig. 5E). The microvilli have a mean diameter of 0.062 μm (SD = 0.002, n = 20), giving a surface area of 66.7 μm^2/μm^3 of rhabdom. Occasional rhabdoms show some evidence of rhabdom breakdown or turnover (Hafner *et al.*, 1980) in the form of multivesicular bodies and lamellar bodies (Fig. 5F). Tapetal reflecting pigment, retinular cell shielding pigment, and lipid are present behind the rhabdom layer in a pattern similar to that seen in 'Chorocaris'. At the back of the eye, the retinular cell axons combine to form an optic nerve similar in all respects to that in 'Chorocaris' (Fig. 5D). Once again, the optic nerve travels posteriorly alongside the lateral protocerebrum before joining the brain laterally and terminating in the lamina ganglion.

Type A. Examination of sections of the eye confirms the external observations that the photoreceptor cells are localized in the anterior and lateral regions of the eyestalk (Fig. 6A) and that there is no thoracic eye. In Type A, in contrast to the other two types of postlarvae, the eyestalk contains the neuropile layers of the optic lobes and other anterior protocerebral regions (Fig. 6B). Once again, the retinular cell axons are grouped together to form a distinctive optic nerve. This travels over the surface of the optic lobes to innervate the lamina ganglion (Fig. 6B). Large accumulations of lipid droplets are also found within the eyestalk (Fig. 6A). Unlike the other two species, Type A has crystalline cone cells in some ommatidia, particularly towards the posterior end of the eye (Fig. 6A). In this region the crystalline cones have a fine-grained appearance typical of crustacean eyes, and they abut the layered rhabdom (Fig. 6C). In anterior ommatidia, the rhabdoms extend virtually to the cornea, although the remnants of some indeterminate cells are found distal to the rhabdoms. The rhabdoms are generally square in cross-section (Fig. 6D) and consist of orthogonally orientated layers of microvilli (Fig. 6E). The latter have an average diameter of 0.066 μm (SD = 0.003, n = 20). The volume density of rhabdoms within the photoreceptor layer is about 68%, with a microvillar membrane area of 61.3 μm^2/μm^3 of rhabdom.

Discussion

Structure of the eye

In comparison with other caridean shrimps, the bresiliids described in this paper exhibit a considerable reduction in most of the structures normally found in the decapod eye (summarized in Fig. 7). The ommatidia of most decapod eyes each consist of a corneal facet secreted by two corneagenous cells, a single crystalline cone formed by four cone cells, eight retinular cells forming a single rhabdom, and a number of tapetal cells. In the larval vent shrimps, most of the eye between the cornea and basement membrane is filled with hypertrophied rhabdoms. As in other decapods, the bulk of the rhabdom appears to be formed by seven retinular cells. Although we were not able to identify an eighth retinular cell in the postlarval specimens, a distinct R8 cell has been observed in prezoea larvae of *Chorocaris fortunata* (Gaten, unpubl. data). Most of the cornea is thin, apparently contains no internal lens, and displays an external facet pattern only in Type A. The mixture of hexagonal and square facets is similar to that seen in postlarval oplophorid shrimps during the transformation from apposition to superposition optics (Gaten and Herring, 1995). Apparently, the zoeal eyes of all decapods have hexagonal facets (Nilsson, 1983). If reflecting superposition eyes, with their characteristic square array of facets, represent the primitive condition in adult decapods (Gaten, 1998), then remnants of the square facets might be expected even though these optics
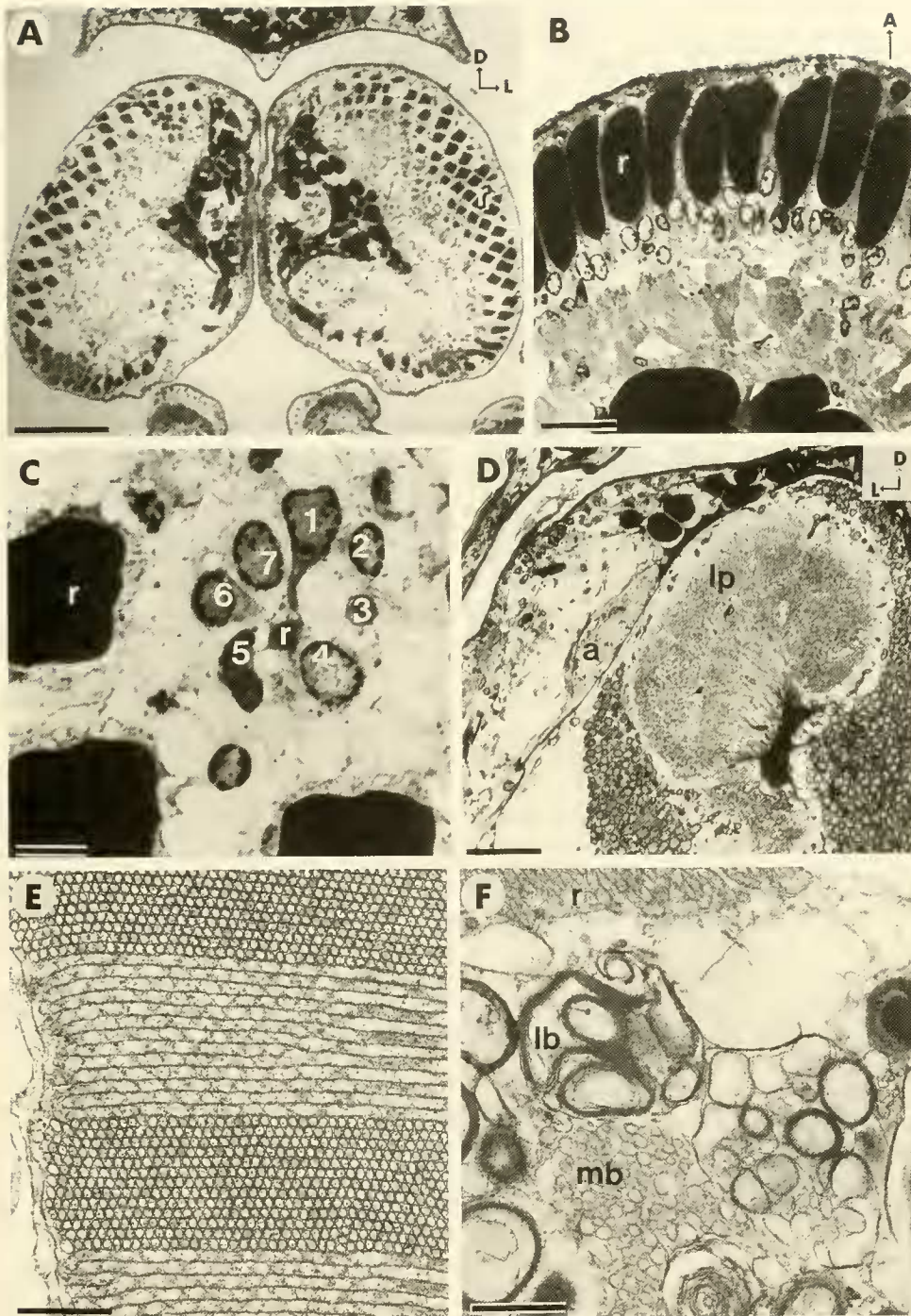
Figure 5. *Alvinocaris* postlarvae (arrows point to Dorsal, Lateral, and Anterior). Light micrographs show the anteriorly directed rhabdoms (r) in vertical transverse sections (A) and in sagittal sections (B) of the eye. (C) The rhabdoms are generally square in cross-section and are surrounded at their base by seven retinular cell nuclei (1–7). (D) Posterior to the eye, the axons (a) remain distal to the basement membrane, still separate from the lateral protocerebrum (lp). Electron micrographs show the layered appearance typical of decapod rhabdoms (E), although there is some evidence of rhabdom turnover (F) in the form of multivesicular bodies (mb) and lamellar bodies (lb). Scale bars: A = 250 μm, B = 50 μm, C = 10 μm, D = 100 μm, E = 0.5 μm, F = 0.5 μm.
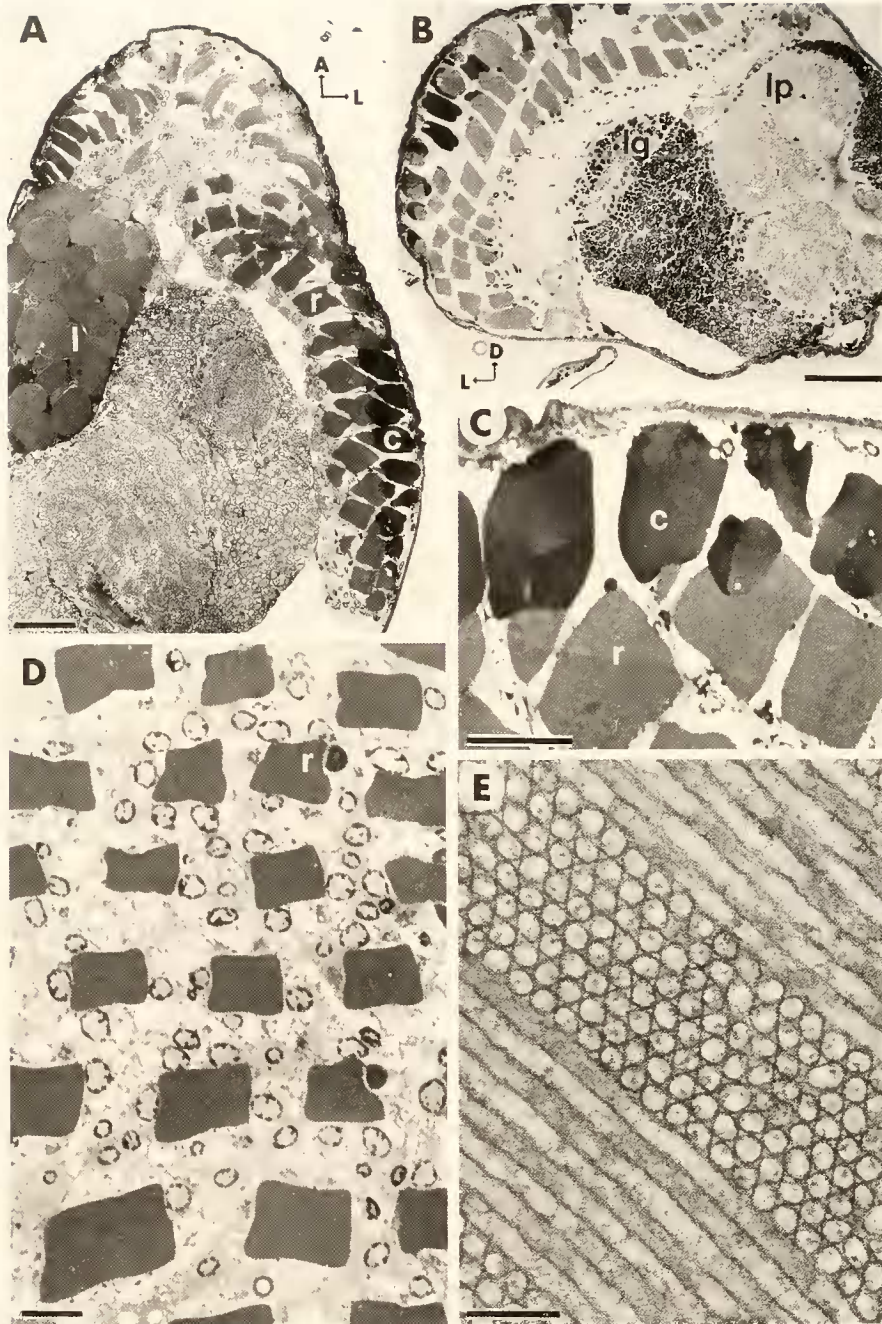
Figure 6.   Type A postlarvae (arrows point to Dorsal, Lateral, and Anterior). (A) In horizontal sections, the eyestalks show a region of rhabdoms extending over the anterior and lateral regions. Crystalline cones (c) are present in lateral ommatidia. Lipid (l) fills much of the eyestalk. (B) This cross-section of the eyestalk shows the presence of lateral protocerebral neuropile (lp) and lamina ganglion (lg) below the basement membrane. (C) Crystalline cones (c) are present in lateral regions of the eye between the rhabdoms and the cornea. (D) The rhabdoms (r) are generally square in cross-section. (E) An electron micrograph showing the orthogonal layers of microvilli in the rhabdom. Scale bars: A = 100 μm, B = 100 μm, C = 50 μm, D = 25 μm, E = 0.2 μm.
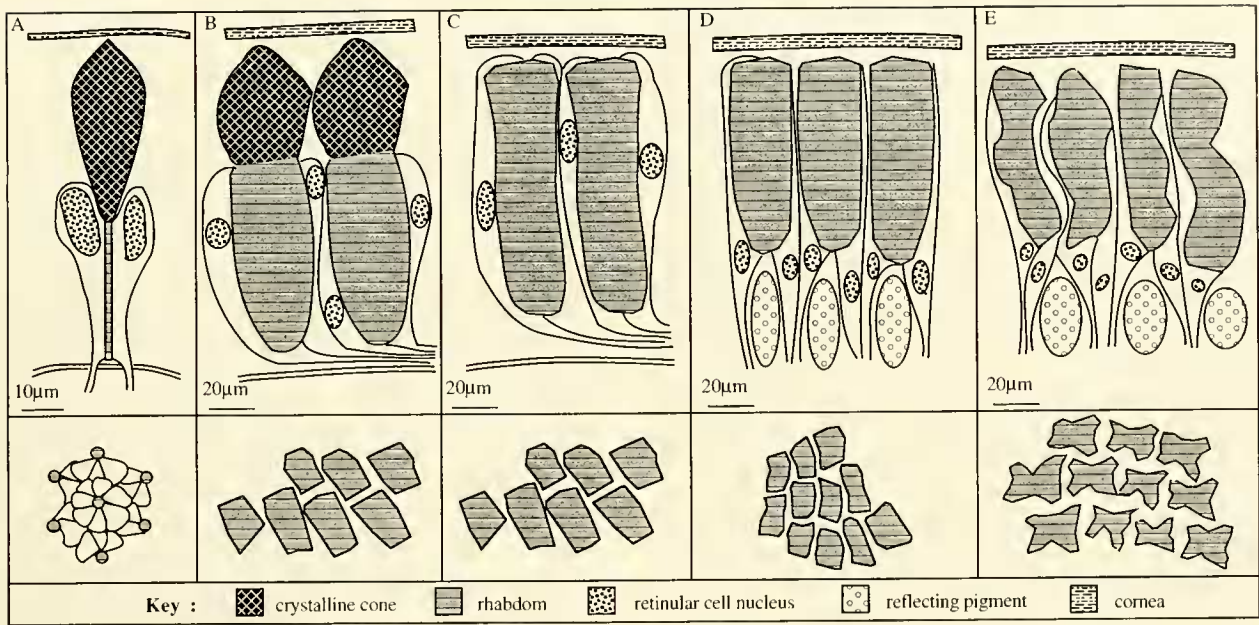
Figure 7. Semi-schematic diagram summarizing the ommatidial structure of the postlarval shrimps described. (A) Prezoea of *Chorocaris fortunata*. (B) Type A lateral ommatidia. (C) Type A anterior ommatidia. (D) *Alvinocaris* type. (E) '*Chorocaris*' type. The distribution of the rhabdoms in transverse section is also shown for each type.

are not used in vent shrimps. In some areas of the eyes of more mature postlarvae, the surface of the cornea bears plumose protrusions that are presumably related to the specialized feeding habits of vent shrimps (Segonzac *et al.*, 1994). Identifiable crystalline cone cells are absent except in the posterior regions of the eye of Type A. Retinular cell shielding pigment is absent from the distal regions of all the eyes examined but is present proximally in reduced amounts. A proximal reflecting layer is prominent, consisting of an extensive array of tapetal cells. An abundance of lipid around the basement membrane probably contributes to the reflecting layer.

The reduction seen in parts of the ommatidia is mirrored to some extent within the Oplophoridae, which are considered to be closely related to the Bresiliidae (Christoffersen, 1990). In the Oplophoridae, eye structure changes with depth. The ommatidia of species from the upper mesopelagic zone, such as *Oplophorus spinosus* (Land, 1976), contain the full range of cells. Species from deeper water, such as *Acanthephyra purpurea*, have very little retinular cell screening pigment, and the rhabdoms interdigitate to form a continuous layer with no optical isolation of rhabdoms (Gaten *et al.*, 1992). In *Hymenodora glacialis*, a species found below the photic zone, the hypertrophied rhabdoms fill the space between the basement membrane and the cornea (Welsh and Chace, 1937).

However, a major departure from the usual decapod

pattern is apparent in the position of the optic neuropiles in '*Chorocaris*' and *A. markensis* postlarvae. The optic neuropiles are normally located within the eyestalks, between the eye and the brain. Only in the Type A postlarvae were the optic ganglia found within the eyestalk, although the ganglia were displaced ventrally by the presence of lateral protocerebral neuropile. Compared to the prominent eyestalks of Type A, the eyestalks in the other taxa are greatly reduced. In the latter cases, the region behind the eye is occupied by the prominent lobes of the lateral protocerebrum, and the optic lobes are displaced posteriorly. This is similar to the arrangement in *Birgus latro*, a species in which the optic lobes are located within the body of the protocerebrum (Sandeman *et al.*, 1993). The function of the protocerebral neuropiles within the anterior lobes of the brain is unknown (Sandeman *et al.*, 1993); in '*Chorocaris*' and *A. markensis* these neuropiles extend forward into the bases of the sensory papillae located on the cornea. The optic neuropiles are often relocated from the eyestalks to the head capsule in the Anomura, Brachyura, and Caridea (Sandeman *et al.*, 1993), but the ommatidia remain at the extremity of the eyestalks. It is the reduction of the eyestalk, bringing the marginal ommatidia close to the dorsal carapace of the cephalothorax, that allows the ommatidia to extend backwards to form the thoracic organ.

The main difference between the postlarval eyes de-

scribed here and the thoracic eyes described in published accounts of the genera *Rimicaris* and *Chorocaris* concerns the appearance of the rhabdoms. The eyes of postlarval Type A and *A. markensis* have the orthogonal layers of microvilli typical of most decapod rhabdoms, with all of the microvilli closely packed and of similar diameter (ranging from 0.062 to 0.067 µm). In 'Chorocaris' postlarvae, the microvilli are larger (about 0.079 µm in diameter) and, although the rhabdoms lack the regular orthogonal arrangement of the layers, the individual microvilli are neatly packed. In contrast, the rhabdoms of the adult eyes described so far (O'Neill *et al.*, 1995; Nuckley *et al.*, 1996; Lakin *et al.*, 1997; Kuenzler *et al.*, 1997) contain larger microvilli (0.09 to 0.12 µm in diameter) that generally lack the orthogonal layering and often show vesiculation towards the edge of the rhabdoms. This unusual appearance of the rhabdoms could reflect some degenerative process occurring in the adults or it could indicate light-induced damage. In deep-sea species, short exposures (as little as 10 s) to daylight can initiate irreversible damage. Although the full morphological impact is not seen for 24 h or more, changes in rhabdom structure are detectable within minutes of exposure (Shelton *et al.*, 1985). If the searchlights employed by the submersible had initiated such damage, the rhabdoms of animals fixed at the surface might show some structural changes. To resolve this question, it is clearly necessary to obtain adult shrimp that have not been exposed to excess light to compare directly with the postlarval rhabdoms described here.

The volume density of rhabdoms within the retinular cell layer varies from 62% in *Alvinocaris markersis* to 75% in 'Chorocaris'. Similar values—ranging from 60% in *Chorocaris chacei* (Lakin *et al.*, 1997) to 85% in *Rimicaris* sp. (Nuckley *et al.*, 1996)—were recorded for adult vent shrimps. The smaller microvillar diameters and tight packing seen in the postlarval shrimps produce a larger surface area of photosensitive membrane (per unit volume of rhabdom) than has been recorded in the adult shrimps. The values for 'Chorocaris' (50.76 $\mu m^2/\mu m^3$), *Alvinocaris markensis* (66.66 $\mu m^2/\mu m^3$), and Type A (61.34 $\mu m^2/\mu m^3$) are all higher than the values of 30.7 $\mu m^2/\mu m^3$ for adult *Chorocaris chacei* (Lakin *et al.*, 1997) and 40.3 $\mu m^2/\mu m^3$ for adult *Rimicaris* sp (Nuckley *et al.*, 1996). Nevertheless, the total volume of the rhabdoms is much smaller in the postlarval shrimps than in the adults, making it unlikely that the sensitivity of the eye is any greater in the postlarval shrimps than in adult *Rimicaris exoculata* (Pelli and Chamberlain, 1989).

Optics

The image in decapod eyes is normally focused by the cornea with its internal lens and by the crystalline cone (*e.g.*, Gaten, 1994). In the eyes of vent shrimps, the crystalline cone is absent in all but the smaller postlarval stages, and the cornea is thin and appears to lack an internal lens. Although there is no mechanism for forming a focused image, there may be some directional sensitivity due to the optical isolation of individual rhabdoms. In deep-sea oplophorids such as *Acanthephyra purpurea*, the rhabdoms interdigitate and are contiguous (Gaten *et al.*, 1992), so there can be no optical isolation of the ommatidia. In the eyes of *Alvinocaris markensis* postlarvae, the anteriorly pointing rhabdoms in the anterior eye have an inter-ommatidial angle of about 3° and are separated from one another by a layer of cytoplasm. As a result, any incident rays at angles up to 12.5° from the ommatidial axis will be retained within the rhabdom, assuming that the refractive indices of the rhabdoms and the surrounding retinular cells are similar to those of other decapods (*e.g.*, Gaten, 1994). The presence of reflecting and shielding pigments behind the rhabdoms may contribute to optical isolation of the rhabdoms. Although most deep-sea crustaceans retain the capacity for all-round vision, the orientation of the rhabdoms in a single direction (anteriorly in *Alvinocaris markensis* and dorsally in *Rimicaris exoculata*) is not unique. Most common, however, when crustacean eyes are highly directional (Land *et al.*, 1979; Land, 1989) is that the visual systems are specialized for upward vision in specimens found at the limit of the downwelling irradiance. Similarly, the presence of highly directional eyes in *A. markensis* and *R. exoculata* suggests that they are specialized for detecting dim light sources from anterior or dorsal directions respectively.

Although the lack of sophisticated optics suggests that image formation is not particularly important in vent shrimps, any directional sensitivity is likely to be relevant to their behavior. The hydrothermal vents are located well below the depths to which light penetrates, but it has been suggested that vent shrimps may be able to see the black-body radiation associated with the heated plumes (Van Dover *et al.*, 1989, 1994; Pelli and Chamberlain, 1989). The relative development of the anterior and thoracic eyes suggests that the vent shrimps may rely on visual cues to maintain their orientation with respect to the vent. Postlarval specimens seeking a vent site may be aided by the possession of anteriorly directed rhabdoms. After settlement, the developing stages of *Rimicaris exoculata* lose the separate corneas of the anterior eyes, whilst the thoracic eye becomes more prominent in the adult. The adults of this species swarm around the base of the vent chimneys, and the presence of only thoracic eyes suggests that these organs are used solely to view the light emitted from the vent (Van Dover *et al.*, 1989, 1994). In contrast, the other genera are less dependent on the vents (Segonzac *et al.*, 1994) and so do not rely solely on the thoracic

organ for location of, and orientation toward, the vent. An alternative explanation may be that the species with more prominent anterior eyes are those that do not form dense swarms, whereas species such as *R. exoculata*, whose anterior ends are buried under swarms, rely on dorsal eyes (S. Chamberlain, pers. comm.).

The presence of orthogonal layers of microvilli in decapod rhabdoms is generally associated with the analysis of polarized light. Such an arrangement was found in the Type A and *Alvinocaris markensis* postlarvae, although in the 'Chorocaris' postlarvae the arrangement of layers was less regular. Such differences may be depth-related, or they may be associated with the development of the shrimps. In oplophorid shrimps, sensitivity to polarized light may be present in animals from the upper mesopelagic zone, but absent in those active under aphotic conditions (Gaten *et al.*, 1992). This would imply that the early postlarvae were living at shallow depths where the analysis of polarized light would be advantageous. Unfortunately we have no information about the depths at which the early developmental stages are found, although all of the postlarvae in this study were caught in the same depth range (2000 m to 3050 m). Alternatively, it may be that all larval and postlarval decapods have orthogonal layering of the rhabdoms, but that it is lost in the later stages of species for which the analysis of polarized light confers no advantage.

Life history

One of the most intriguing questions concerning vent shrimps is how they maintain a viable population at an existing vent while employing a dispersal strategy that enables them to locate and colonize new vent sites. The eggs are microlecithal, and they hatch at the zoeal stage with apposition eyes (P. J. Herring, unpubl. obs.). In contrast, the zoeal stages of shrimps with macrolecithal eggs are completed within the egg, and the eye of the newly hatched postlarva is capable of using superposition optics (Gaten and Herring, 1995). Through the generosity of Dr. M. Segonzac (IFREMER), we obtained prezoeas of the related *Chorocaris fortunata* from eggs about to hatch. The eyes of these very late embryos have crystalline cones (Fig. 7) and appear to be capable of using apposition optics (supported by recent observations on laboratory-hatched first zoeas: P. J. Herring, unpubl. data). This finding suggests that these shrimp could have passed through their early developmental stages in a photic environment; furthermore, there is some evidence that the lipid distributed throughout the bodies of the shrimps is of planktonic origin (Dixon and Dixon, 1996). The fact that the eyes of the Type A postlarvae described here have crystalline cones suggests that they, too, may have spent their early

life history in the photic zone. Although we have no definitive evidence, we postulate that the postlarval shrimps were returning to vent sites following a planktotrophic zoeal phase.

In view of the large distances involved and the difficulties inherent in locating a vent site, it seems likely that the sense organs of postlarval vent shrimps are adapted for the detection of vent sites, whether by sensing light, temperature, or sulfide concentration. It has been suggested that the eyes of postlarval shrimps are primarily concerned with assembling the large array of photoreceptors found in the eyes of the adult (S. Chamberlain, pers. comm.). However, the optically isolated and anteriorly pointing rhabdoms in the anterior eye imply that it is adapted to enhance directional sensitivity, whilst the reduced optics are typical of the eyes of animals that need to maximize sensitivity at the expense of resolution. We suggest that the eye of the postlarval vent shrimp functions as an extremely sensitive and highly directional photoreceptor, adapted to detect quanta emitted from a hydrothermal vent.

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